

## CHROMOSOME CONSTITUTIONS OF MEXICAN AND GUATEMALAN RACES OF MAIZE

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During the past year attention was devoted mainly to study of the chromosome constitutions of plants of various races of maize grown in Mexico, Central America, and the Antilles. The purpose of the investigation was to determine whether differences in chromosome constitution among plants of a race and among plants of different races would reveal something about the origin of races and the degrees of their genetic relationship. Evidence that such information might be useful for this purpose had been derived from a preliminary study conducted with some of the well defined races of maize of Venezuela, Ecuador, Bolivia, and Chile, reported in Year Book 58. The investigation to be reported here was undertaken at the invitation of the Rockefeller Foundation and in collaboration with Dr. E. J. Wellhausen, who is in charge of the maize program within the Foundation.

Dr. Wellhausen and his collaborators had made an intensive study of maize grown in Mexico and Central America. The types grown within this large area are exceedingly diverse with respect to morphological and physiological characters expressed in different parts of the plant and in the ear and kernel. Through a comparative study of these many types, Dr. Wellhausen's group devised a system

of classification that considered the probable genetic relationships. A number of classes were proposed, each incorporating a distinctive set of plant and ear characters. Many of the maize types could be placed in one or another of these classes, either fitting closely into the scheme of a class or conforming to it in many though not all characters. Each such idealized class was given the status of a "race" of maize, and an identifying name. The maize that corresponded most closely to the scheme of a class was considered the purest example of the racial type.

Some of the races so classified are restricted in distribution, each being encountered only in a specific locality. Others are grown over a wide territory. Within one region, several different races may be grown in close proximity. By careful selection of seed, these several races may be maintained year after year, even in the same field, without suffering marked alteration of type as a consequence of hybridization. It is also apparent that races extensively grown in one locality have been introduced into new localities, often distantly removed, where their racial characters have either been maintained by careful seed selection or been altered by hybridization with maize of other types grown in the new localities.

It seemed evident that some of the present-day races of maize must owe their origin to just such hybridization, some probably occurring centuries ago and some in more recent times. It was thought that analysis of chromosome constitutions in plants of such races, and in the suspected parents, might confirm their hybrid origins. The past year's study yielded some very good evidence in support of these conjectures; examples will be considered later.

The plants whose chromosomes were to be examined came from kernels produced by plants belonging to different races. The seed representing each race was obtained from a locality where the plants exhibit the combination of characters considered most representative of the race, as defined above. The selections were as follows: 25 races from Mexico; 17 from Guatemala; 1 each from Honduras, Nicaragua, and Costa Rica; 6 from Cuba; and 1 each from Haiti, Martinique, and Trinidad. The names and geographical sources of the Mexican and Central American races are given in table 16.

All the selected races were grown in the summer of 1959 at the agricultural experiment station at Chapingo, Mexico, operated by the Rockefeller Foundation. As material for examination of chromosomes at the meiotic prophase, young tassels were removed from six plants grown from seed of each selection. These were placed in an alcohol-acetic acid fixative, which was replaced with 70 per cent alcohol after 48 hours; they were then stored in a deep-freeze unit until needed for chromosome examination. Temporary smear preparations of microsporocytes at pachytene, diplotene, and diakinesis stages, stained with propiocarmine, were examined. Permanent preparations were not made. It was impossible for one investigator to attend to them within the period of time allotted to the survey; and, as there was no advance assurance that the study would reveal anything of importance, technical assistance was not obtained. Experience

showed, however, that it is advisable to have permanent preparations. It would have been instructive to make direct comparisons of the chromosome constitutions of certain plants that were examined at very different times.

The main object in examining the chromosomes was to determine the presence or absence of knobs at the knob-forming regions in each of the 10 chromosomes that compose the haploid set in maize. (Knobs are deep-staining, heterochromatic components of the chromosomes.) If a knob was found at any one of these locations, it was then necessary to determine its size, shape, and stainability, and also to find out whether both homologues carried a knob at that location. If they did, the next step was to discover whether the two knobs were alike, or in what ways they differed. If B-type chromosomes were present, the number was ascertained. Note was taken also of any conspicuous alteration in chromosome organization, such as a rearrangement of easily recognizable type, an enlarged chromomere at a particular location, or other unusual modification.

In many plants, the study was complicated by the presence of a large number of knobs, all or most of which were fused with one another in many cells at the pachytene stage. It was often necessary to examine hundreds of cells before finding one in which the type of knob present at a particular location could be identified. In the strain from Trinidad, fusion of knobs was so extensive and persistent that no accurate determination of the type of knob at each knob-forming region could be made in any of its plants. In a few other strains, similar difficulty was occasionally encountered, but only in some plants and with regard to certain knobs. In chromosomes of most plants, it was possible to learn what type of knob had been produced by each knob-forming region. Knob size and shape were recorded from cells in the late pachytene stage, but it was

TABLE 16. The Races of Maize Whose Chromosomes Were Examined, and the Place Where Each Was Collected

Name of Race	Where Collected
A. Mexico:	
Arrocillo Amarillo	Zaragoya, Puebla
Bolita	Etla, Oaxaca
Cacahuacintle	Toluca, México
Celaya	Irapuato, Guanajuato
Chalqueño	Chalco, México
Chapalote	El Fuerte, Sinaloa
Comiteco	Comitán, Chiapas
Cónico	Toluca, México
Cónico Norteño	El Sotelo, Guanajuato
Harinoso de Ocho	El Fuerte, Sinaloa
Jala	Jala, Nayarit
Maíz Dulce	El Sotelo, Guanajuato
Nal-Tel	Mérida, Yucatán
Olotillo	Tuxtla Gutiérrez, Chiapas
Olotón	Las Casas, Chiapas
Olotón	Ojo de Agua, Chiapas
Palomero Toluqueño	near Toluca, México
Pepitilla	near Iguala, Guerrero
Reventador	Ejido de Tuxpan, Nayarit
Tabloncillo	near Tequila, Jalisco
Tehua	near Comitán, Chiapas
Tuxpeño	Gutiérrez Zamora, Veracruz
Vandeño	Escintla, Chiapas
Zapalote Chico	Tehuantepec, Oaxaca
Zapalote Grande	Colonia Lázarus Cardenas, Chiapas
B. Guatemala:	
Comiteco	San Raymundo, Guatemala
Dzit-Bacal	San Antonio Monjas, Jalapa
Imbricado	Tecpán G., Chimaltenango
Imbricado	Tecpán G., Chimaltenango (another collection)
Nal-Tel Armarillo, Tierra Baja	Ipala, Chiquimula
Nal-Tel Blanco, Tierra Alta	Chequiral, Quetzaltenango
Nal-Tel Blanco, Tierra Baja	Ladrillo Barrio, Baja Verapaz
Nal-Tel de Ocho	Comalapa, Chimaltenango
Nal-Tel de Ocho	Santiago Buena Vista, San Marcos
Olotón	San Martín, Quetzaltenango
Quicheño Precóz	Uspantán, El Quiché
Quicheño Tardío	Cantón Sasiguan, Sololá
Salpor	Cheluj, Quetzaltenango
San Marceño	Concepción, Huehuetenango
Serrano	San Sebastián, Huehuetenango
Tepecintle	Panzos, Alta Verapaz
Tuxpeño	Sayaxche, Petén
C. Honduras, Nicaragua, and Costa Rica:	
Salvadoreño de Costa Rica	Santa Cruz, Guanacaste, Costa Rica
Salvadoreño de Honduras	Nueva Ocotepeque, Honduras
Salvadoreño de Nicaragua	Juicalpa, Nicaragua

necessary to observe the early diplotene stage also in order to discover whether a particular knob was present in only one homologue or in both. It is not always possible to make such a determination at the late pachytene stage.

A truly objective method of determining knob size and shape is not possible. The size and shape of a knob at late pachytene depend on several factors. The first of these is the capacity of a knob-forming region to produce a knob of a particular size and shape, but secondary factors may modify the expression of this capacity. In some plants, the chromosomes at late pachytene are very long, and each of the knobs is extended, often being long and relatively slender. In other plants, the late pachytene chromosomes are much shorter, and the knobs are correspondingly condensed and widened. Growing conditions may affect the composition of the chromosomes, and this influence also is reflected in length of chromosome, size of chromomeres, and size of knobs. When plants are growing poorly, the chromosomes, including the knobs, are sometimes thin and may stain weakly. Despite such factors that alter the form of knobs, extensive experience in observing chromosomes and their knobs at pachytene and later meiotic stages makes it possible to judge conditions in a particular plant and their effect in modifying knob appearance.

To minimize bias in determining knob constitution in plants of the same selection, the six plants from each selection were not examined in sequence. Results being obtained with material from one plant were not compared with the records for sister plants until after the analysis of the plant's knob constitution had been completed. Although the method of estimating knob type was purely subjective, a considerable degree of consistency was evidently obtained. This fact was not fully appreciated until all the data had been collected and the geographical distribution of each knob type plotted on maps. It was then apparent that there must have been a

large measure of consistency in the evaluations. Otherwise, a number of previously unsuspected correlations between a recorded knob type and its geographical distribution would not have appeared on the maps.

The chromosomes of maize growing in different parts of the world have been examined by many investigators. Their findings have demonstrated a marked degree of conservatism in the linear organization of the chromosomes. There is no evidence of perpetuation of a reciprocal translocation. Perpetuation of readily detectable inversions also must be rare. Only one such inversion is known to have persisted. The inverted segment is composed of the distal two-thirds of the short arm of chromosome 8. This inversion is readily detected in plants that are heterozygous for it. Such plants were found in four of the races examined this past season. Notably, all these races came from central Mexico. It had previously been observed in plants of one particular race now growing in Bolivia. Since the inverted segment was the same in all plants, it may be suspected that this one race in Bolivia received a chromosome 8 from maize introduced from central Mexico. Other knobs present in chromosomes of this race also support the supposition.

One other type of chromosomal modification was found to be widely distributed. It is carried by chromosome 10 and in the past has been designated "abnormal chromosome 10." "Abnormal chromosome 10" is readily identifiable because it has an extensively modified segment at the distal end of its long arm. This segment greatly increases the length of the arm, and close to its distal end there is a very large knob. "Abnormal chromosome 10" appears in maize plants grown in the southwest part of the United States, in various localities in Mexico, and in Central America, and was found in some plants of a Cuban race. It had been encountered in Ecuador and Peru, but only in plants from several isolated localities. Its very wide distribu-

tion in North America and its apparently limited distribution in western South America suggest that it may have been introduced into South America in recent times.

The components of organization of the maize chromosomes that do show marked grades of difference in different plants of a race or in plants of different races are the knobs, the nucleolus organizer, and some chromomeres whose locations are quite specific. The nucleolus organizer and these chromomeres may be much enlarged in plants of some races. The different types of expression shown by any of these components of the chromosome complement are genetically controlled; each type is heritable. Thus, they are useful in tracing relationships between plants of different races growing either in the same region or in widely separated regions. In the present study, attention was concentrated on the knobs and on one particular chromomere. Differences in appearance of other specific chromomeres were very effective for the purpose of this study, but the fact was not fully appreciated until after many plants had been examined. Therefore the notes on these other chromomeres are incomplete. The same is true of differences in appearance of the nucleolus organizer, whose size may range from very small in plants of some races to extremely large in those of other races.

Knobs are produced by knob-forming regions at particular locations in each of the 10 chromosomes of maize. The regions are short, and they are compound in the sense that each component of a knob-forming region acts independently in producing knob substance. Differences in knob-forming capacity of components within a region are responsible not only for the length of a knob but also for differences in width along its length. The combined result is a knob having a particular size and shape. With regard to length alone, very great differences may be expressed in one knob-forming region. As

an illustration we may take the knob-forming region at the end of the short arm of chromosome 9. Its capacity to produce knob substance ranges from apparently none through an ascending series that results in the production of a tiny knob, a small knob, a medium-sized knob, a large knob, or a very large knob. A very large knob may extend from the end of the short arm approximately one-third the length of the arm as measured at the pachytene stage. Such a knob, since it is not only long but also very wide, is truly tremendous.

Although there are these large differences in knob-producing capacity at a particular location, any one expression of capacity is constant, in that it continues to produce the same type of knob generation after generation. This being so, a question arises as to the origin of the very different kinds of expression. Because of the types of knobs observed, and their individual distributions in the examined races in both North and South America, I am led to consider the possibility that cultivated maize may have had several independent origins, from plants whose knob-forming regions had distinctly different capacities for producing knob substance. One cultivated type may have originated from plants in which all the knob-forming regions had such limited capacities that the derived maize had no detectable knobs or only a small knob in one or several of the knob-forming regions. Another type may have originated from plants whose knob-forming regions were less limited in capacity, so that the chromosomes of the cultivated plants had either small or medium-sized knobs. Still another may have originated from plants whose knob-forming regions were able to produce large amounts of knob substance; in this cultivated type large knobs would be present. On this basis it may be reasoned that much of the maize now being cultivated in western Mexico, the west coastal regions of Central America, and

northern Venezuela was derived from original types in which most of the knob-forming regions had well developed capacities for producing knob substance; and that the maize now being grown in west central Guatemala, on the contrary, was derived from an original type whose knob-forming regions were very limited in capacity. If the study of knobs in present-day maize were extended, it might be possible to infer the nature of the knob complexes in several other early types of cultivated maize.

The origin of cultivated maize is a mystery. No form of wild maize is known from which cultivated maize could have arisen directly; and none of the theories proposed to account for the origin of cultivated maize has received general acceptance. Therefore, the hypothesis outlined above regarding possible independent origins of cultivated maize cannot be supported directly, even though much evidence to suggest it has developed from the study of knob constitutions in present-day maize. The types of knob complexes in different strains of the two closely related wild genera *Euchlaena* and *Tripsacum* should be explored thoroughly in order to determine whether or not they reflect differences in capacity of the knob-forming regions comparable to those discussed above, and, if so, whether or not the different complexes are geographically localized. If this should prove to be true, it would support the above-proposed theory, not necessarily in its present form but in some form that might aid in interpreting the origin of cultivated maize and in elucidating the derivation of the different knob complexes so clearly depicted in present-day maize. Since the over-all organization of the chromosomes is much alike in *Euchlaena* and maize, and since the two genera may be crossed readily, interchange of segments of chromosomes, including knob-forming regions, undoubtedly has occurred between them. Therefore, the knob constitutions of *Euchlaena* and maize growing in the same

region should be compared, in a search for some evidence of the part *Euchlaena* may have played in introducing components of particular knob complexes into maize.

The constancy of the knob-forming capacities of particular knob-forming regions was spectacularly revealed in the preliminary study of races of maize of western South America. In races from the high Andean valleys of Ecuador, Bolivia, and Chile, previously under the control of the Inca Empire, one particular knob complex was present in plants of nearly all races examined. In the examined races from the high Andean valleys of Venezuela, beyond the control of the Inca Empire, a very different complex of knobs was present. It is well known that in the past each Indian tribe carefully preserved its own types of maize; and this may account for the extension of one particular complex of knobs, the Inca-Andean complex, throughout such a vast territory. Within this territory, however, a few exceptional races were found whose chromosomes had types of knobs other than those belonging to the Inca-Andean complex. Investigators had concluded, on the basis of morphological characters, that the exceptional races contained foreign germplasm, and that in two of them it had probably been introduced from Mexico. The types of knobs in plants of these two races support their deduction. On the basis of evidence from the recent study with Mexican and Central American maize, it is suspected that in one of the two races, Pisinkalla of Bolivia, the foreign germplasm was derived from maize of central Mexico, although this germplasm is now much diluted with that of indigenous Inca-Andean maize. The types of knobs found in the other race, Conguil of Ecuador, suggest that its foreign germplasm may have been derived from maize introduced from the southern part of the state of Chiapas, Mexico, although here, too, dilution with Inca-Andean germplasm is evident.

The study of knob constitutions in the

lowlands of these same South American countries revealed that Inca-Andean maize had also contributed to the development of new races in those regions. Along the eastern as well as the western slopes of the Andes there is evidence of extensive mixing of the Inca-Andean germplasm with that of indigenous or introduced maize of the lower lands. In some of the lowland areas, such as in northern Bolivia, the Inca-Andean germplasm predominates, whereas in the southeastern lowlands of Bolivia the Inca-Andean germplasm is much diluted by that from other sources, one of which appears to be the same that contributed to maize now being grown in the Antilles. In the northwest coastal region and adjacent inland valleys of Ecuador, the Inca-Andean germplasm has become mixed with germplasm that seems to be the same as that of maize now growing in parts of Central America. Farther south, germplasm from other sources has been mixed with that of Inca-Andean origin. In Chile, some of the germplasm apparently stems from Central America and Mexico, but a still unknown source also has contributed to the mixed germplasms of the races growing in the western and coastal parts of Chile.

It is now quite evident that a knowledge of knob constitutions can reveal how foreign maize introduced into a given territory has contributed to the origin of new races, and sometimes it is also possible to infer the source of the introduced maize. The regions where foreign germplasm has been extensively introduced are those in which the human population and culture are mixed, and probably in these regions many introductions have occurred in recent times. Thus, migration of plants with particular germplasms along certain pathways, and hybridization between them in regions of contact, as well as foreign introductions and subsequent hybridizations with indigenous maize, must have contributed to the origin and spread of many present-day races of maize.

The method of sampling in the earlier study of South American maize was quite different from that employed in the recent study. In the earlier work, the examined plants of any particular race were derived not from one locality but from several different localities in a country where the race was grown. Thus there was a wider sampling of plants within any given area. In my opinion this method should be followed in the future, for it is more effective in revealing the migration of a particular knob (and the chromosome segment carrying it) throughout a region, and its penetration into different races growing in the region. By this method it was learned that some segments of chromosome pass through racial boundaries and filter along certain paths. Knowledge of such migration and filtration is important for an appreciation of the genetic contribution of particular segments of chromosome to the characters shown by races within a region. The method also revealed the extensive migration of the B-type chromosome throughout a certain area, passing through racial "boundaries" as if no such boundaries existed. Since the B-type chromosome does not alter genetic expression of racial characters, it is easy to imagine how it might infiltrate all races within a territory. There would be no selection against it by the methods employed to preserve a racial type, that is, to preserve intact a given set of characters considered desirable by the grower.

In the Central Mesa of Mexico, which has a long cultural history, maize with several distinctive knob complexes must have been introduced early, for components of each of them are distributed among plants of different races now growing throughout a wide area in central Mexico. It appears that early hybridization between plants having these distinctly different original knob complexes contributed to the origin of some of the races that have been established in this region for many centuries. Archaeological evidence and

tradition attest to the antiquity of such races. One of the knob complexes of this area seems to have been derived from an original type of maize in which knobs were absent; it may be designated the "no-knob" complex. The present-day race, Cacahuacintle, may have much of that original germplasm. Plants of this race which were examined had very few knobs, and when a knob was present it was usually heterozygous; that is, there was a knob in one chromosome but none at the same location in the homologue.

The production of relatively large knobs at most of the knob-forming chromosomal regions characterized another original knob complex entering into maize of this area. Plants with this complex also contributed to the origin of races of maize now growing in the west central and northwest parts of Mexico. A third complex resembled that now predominating in a restricted area of the central highlands of Guatemala. It was characterized by the production of relatively small knobs at many of its knob-forming regions and no knobs at others. It may be designated the "small-knob" complex. In none of the examined races of central Mexico does this small-knob complex predominate, but components of it are distributed among many of them. The same statement applies to what may be the remnants of a complex composed of extremely large knobs. Exceedingly large knobs produced at each of three different knob-forming regions were occasionally encountered in plants grown in this area.

It appears, then, that maize having distinctly different knob complexes entered into the formation of present-day races of the Central Mesa of Mexico. The contribution of each complex to the origin of the different races cannot be stated precisely, as the sampling in the area has been much too restricted. In the sample of the Palomero Toluqueño race, however, components of the large-knob complex predominated, although the germplasm that

contributed them was somewhat diluted by others carrying the no-knob complex, the small-knob complex, and the very-large-knob complex. Plants of the race Cacahuacintle, growing in the same region, had very few knobs, as was mentioned earlier. These two races are considered by Wellhausen and his collaborators to be rather direct descendants of two ancient races. They conjecture that the two original races gave rise, by hybridization, to some of the most productive maize that has been grown in the Central Mesa for many centuries. The knob constitution of one such conjectural hybrid, the present-day race Cónico, conforms with this assumption. Its plants have some of the large knobs that are present in Palomero Toluqueño, but their germplasm is much diluted by that of the no-knob complex. In fact, components of all the above-described knob complexes were found to be present to various degrees in plants of each of the five examined races of maize of the Central Mesa.

Only one sample of maize now growing on the east central coast of Mexico was examined, of the race Tuxpeño. Therefore no conclusions can be drawn about the different types of germplasm that may be present in this general area. Nevertheless, it was clear from the knob constitutions of these plants that they had some germplasm that was either absent or not very prevalent in the examined plants of central Mexico but was found to be extensively distributed throughout Cuba. Judged by knob constitutions, the maize of Cuba gives little evidence of close affinity with that of either central or western Mexico. On the basis of morphological characters alone, it is assumed to have germplasm in common with maize of the east coast of South America. The knob constitutions of that maize have not been examined; but, on the assumption that Cuban maize contains much germplasm derived from eastern South America, it may be conjectured that plants of the race Tuxpeño, growing

in the state of Veracruz, also have some of that germplasm.

The three examined races of maize grown in the Bajío, north of the Central Mesa of Mexico—Cónico Norteño, Maíz Dulce, and Celaya—appear to share germplasm with races that grow to the west and north of that region. In general, knob constitutions in plants of these races are much like those of the races Chapalote and Harinoso de Ocho from the state of Sinaloa, the race Reventador from the state of Nayarit, and the race Tabloncillo from the state of Jalisco, although some minor differences characterize the knob constitutions in the different races. Relatively large knobs, of similar type at any one region, are produced by many of the knob-forming regions in plants of these races; and, for the most part, the expressions of homologous knob-forming regions are alike. This relationship is in contrast to the high degree of heterozygosity of knob expression seen in the races grown in the Central Mesa. Nevertheless, neither in the races of the Bajío nor in those of the northwest and west central coast was any plant found that showed complete homozygosity of knob formation. Some dilution of the predominant knob complex was observed in each plant. A small amount of dilution by the small-knob complex and the no-knob complex was evident in plants of the Bajío, and a small amount of dilution by the no-knob complex, or by one having very few knobs, was apparent in plants of the northwest and of the west central coastal region.

In the state of Nayarit one race, Jala, whose distribution is restricted almost exclusively to the small Jala valley, is considered by Wellhausen and his collaborators to have originated through hybridization between maize introduced into this valley and maize that was being grown there. The foreign maize is assumed to have come from the southern part of the state of Chiapas, Mexico, or from an adjacent region in Guatemala. Some of the

knobs in plants from western Mexico and from southern Chiapas are alike, and many of the knobs in the Jala plants are of the type commonly found in samples from both regions. In the Jala plants, however, there is one particular knob of a very distinctive type, which was otherwise encountered only in plants from southern Mexico, southwest Guatemala, Honduras, Nicaragua, and Costa Rica, where this type of knob is the one commonly expressed by the particular knob-forming region. The presence of this knob in a place so distantly removed from the area where it regularly appears supports the above-stated assumption about the origin of the race Jala.

Of all the areas examined in the recent study, southern Mexico and Guatemala proved the most interesting. This was so partly because of the more extensive sampling in that region, which made it possible to follow more closely the migration of components of different knob complexes. At least four recognizably different knob complexes have contributed to the races of maize now growing there. One of them is characterized by the production of very large knobs at many of the knob-forming regions. It is the predominant complex in maize growing along the southwest coast, from the state of Oaxaca in Mexico to Costa Rica, the southernmost region from which a sample was examined. The northward flow of components of this complex into maize of the southern highlands of Guatemala could be traced, as well as the gradual dilution of the complex by components of the other knob complexes that predominate in the interior of Guatemala. Two distinctly different complexes predominate in the interior. One appears to be the Inca-Andean complex. No plants were found that had only this complex, but its components are most highly concentrated in maize of the west central highlands. Components appear also in maize grown to the east of this region and

in maize grown to the north, in the contiguous state of Chiapas, Mexico; but in both these areas the complex is very much diluted, and other complexes predominate. The predominant knob complex in maize of the central highlands of Guatemala is one in which only a small or medium-sized knob is produced at many of the knob-forming regions. Components of this complex have migrated into maize of adjacent regions, and also into the one race from Honduras that was examined. As might be expected, components were found in maize of southern Chiapas. In all these contiguous areas, however, the complex was much diluted. As was mentioned earlier, components of this complex were also found in central Mexico.

One race growing in Guatemala, *Imbricado*, has a very limited distribution. It is considered to be related to the race *Palomero Toluqueño* of the Central Mesa of Mexico, discussed earlier, and the knob constitutions of its plants support this assumption. Two very distinctive knobs were found that otherwise were encountered only in plants from central Mexico, one of them only in the race *Palomero Toluqueño* and other races growing in proximity to it. The evidence suggests that this race may well have arisen by hybridization of indigenous maize with maize introduced into Guatemala from the Central Mesa of Mexico.

Only one sampling of maize from the northeastern lowlands of Guatemala was examined, of the race *Tuxpeño*. The knob constitutions of plants of this selection were similar to those of *Tuxpeño* plants from Veracruz, Mexico, discussed earlier.

Knob constitutions were examined in six selections of the race *Nal-Tel*, five of them native to Guatemala and one native to the coastal region of Yucatán, Mexico. The characters displayed by plants of this race are considered by Wellhausen and his collaborators to be primitive. Plants of all six selections exhibited these assumedly primitive characters, but the

individual selections differed in some other respects. Examination of chromosomes from these different selections yielded no clear evidence of the presence of one particular type of knob constitution that might be considered characteristic of the race as a whole. Instead, the constitutions in five of the six selections reflected the predominant knob complexes found in plants of other races growing in the same general region. The sixth selection, that from Mérida, Yucatán, was so far removed geographically from other maize examined that no conclusions could be drawn about the relation of its knob constitution to those of other races growing in the same vicinity. Although consistency in type of knob constitution was expressed among the plants of each selection of the *Nal-Tel* race, very great differences were observed among the different selections. Clearly, the predominant characters that have caused these plants to be assigned to the same race need to be explored by genetic techniques. Racial classification of plants growing in widely different regions, based on similarity of morphological characters and presupposing a high degree of similarity in genetic constitution, is not well supported by cytological evidence in this instance, although it is so supported in some of the other cases.

#### *General Conclusions*

Examination of chromosome constitutions in maize now growing in Mexico and Guatemala has revealed an extensive mixing of different germplasms in many regions of this large area. The mixing has resulted through the flow of particular germplasms along certain paths and through direct introductions of maize having one type of germplasm into localities where other types were predominant. Some of the introductions must have occurred long ago, for components of the introduced germplasm have been spread over a wide territory. Others probably occurred in relatively recent times, because

the influence of the introduced germplasm is still confined to a restricted locality.

In the Central Mesa of Mexico, as was mentioned earlier, three or more original types of germplasm are extensively mixed. In Guatemala, not much direct introduction of foreign maize seems to have occurred. An early introduction of Inca-Andean maize into one part of the western highlands is suspected, as well as a much later one from central Mexico to a locality in the south. Most of the mixture of germplasm in Guatemala appears to have resulted from an inflow of germplasms from surrounding territories. In the highlands, the flow seems to have come from adjoining regions to the south. The flow of germplasm carrying components of the small-knob complex away from Guatemala has apparently been much more restricted. Probably the spread of this germplasm came about either when maize carrying it was introduced directly into a distant region or when maize of an adjacent area, in which components of the germplasm had previously been incorporated, was taken to a new locality.

Flow of particular germplasms along certain paths is well demonstrated by the geographic distributions of types of knobs that are distinctive in some way, either because they have very special size and shape or because they are of a type that appears infrequently at a certain location in the chromosome complement. Plotting the distribution of such knobs on geographic maps, according to the geographic locations of the selections, has produced some striking illustrations of flow. In addition, as was mentioned earlier, these distinctive knobs have sometimes made it possible to infer the probable source of maize that has been introduced into a different locality.

The distribution of the B-type chromosome, in the areas examined in both North and South America, is instructive in several ways. This chromosome is widely distributed in Indian maize of the central

and southwest United States, and also among Mexican maize. It was found to be highly concentrated in some areas of the Andes, and in some lowland regions in Chile. It was not found in the examined plants of the Antilles and was present in plants of only one examined race of Guatemala—Tuxpeño, which is native to the northeastern lowlands. The B-type chromosome is an accessory chromosome containing no genetic components that alter in any yet recognizable way either the appearance or the physiology of a plant. Plants may contain one or more B-type chromosomes, whose presence is revealed only by cytological examination. The chromosome exhibited the same, very distinctive, linear organization in all plants carrying it, thus paralleling the pronounced constancy shown by the normal chromosomes of the complement. Its wide distribution is remarkable. As was explained earlier, however, its flow throughout a population of plants in a given territory could be rapid, and need not be accompanied by a similar flow of genetic components from the normal set of chromosomes. In fact, its independent flow suggests the methods that must have been used in the past to preserve intact the characters of a particular race within a given territory where many different races were grown.

Before concluding, it may be in order to comment regarding the concept of race, lest some misunderstanding arise. The term race has been applied throughout this report in conformity with its usage by Wellhausen and others. It must be obvious from the preceding discussions that the appearance of particular plant, ear, and kernel characters in specific combinations in a large number of plants within a given territory does not carry the implication of established homozygosity of the genetic components responsible for these characters. In fact, some of the examined samples, all selected because they most clearly expressed the combina-

tion of morphological characters chosen to define the race, were highly heterozygous. Even within the same race—for example, the race Nal-Tel discussed earlier—different selections were found to be heterozygous to various degrees and with regard to different chromosomal components. Nevertheless, it is both useful and necessary to classify present-day maize into distinctive races, on the basis of well defined sets of morphological and physiological characters kept together through propa-

gative methods. By means of such classification, it has been possible to apprehend degrees of genetic relationship among plants of different types growing either in one area or in widely separated areas. For a clearer understanding of these relationships, a precise genetic and cytological study of certain races should be undertaken, to determine and compare the types of genetic components that have contributed to the establishment and success of each race.

## BIBLIOGRAPHY

- Balbinder, Elias. See Rudner, R.
- Cocito, C., and A. D. Hershey. Transfer of DNA-glucose from parental to offspring phage T2. *Biochim. et Biophys. Acta*, 37, 543-544, 1960.
- Demerec, M. Frequency of deletions among spontaneous and induced mutations in *Salmonella*. *Proc. Natl. Acad. Sci. U. S.*, 46, 1075-1079, 1960.
- Demerec, M., and J. Sams. Induction of mutations in individual genes of *Escherichia coli* by low X-radiation. *Proc. Symposium on immediate and low-level effects of ionizing radiations*, Venice, 1959 (ed., A. A. Buzzati-Traverso), suppl. to *Intern. J. Radiation Biol.*, London, 1960, pp. 283-291.
- Demerec, M. See also Miyake, T.
- Gay, H. In Chapter V, Morphological organization of nucleus and cytoplasm. In *Biological Organisation, Cellular and Subcellular*, edited by C. H. Waddington, Pergamon Press, London, pp. 110-135, 1959.
- Gay, H. Nuclear control of the cell. *Sci. American*, 202, 126-136, 1960.
- Gay, H. See also Kaufmann, B. P.
- Hashimoto, K. Streptomycin resistance in *Escherichia coli* analyzed by transduction. *Genetics*, 45, 49-62, 1960.
- Hershey, A. D. The production of recombinants in phage crosses. *Cold Spring Harbor Symposia Quant. Biol.*, 23, 19-46, 1958.
- Hershey, A. D. See also Cocito, C.; Koch, G.
- Kaufmann, B. P. Genetic effects of roentgen rays. *J. Am. Dental Assoc.*, 59, 1155-1168, 1959.
- Kaufmann, B. P. Varying patterns of chromosomal fine structure. In *The Cell Nucleus*, edited by J. S. Mitchell, Butterworth, London, pp. 251-263, 1960.
- Kaufmann, B. P., H. Gay, and M. R. McDonald. Organizational patterns within chromosomes. *Intern. Rev. Cytol.*, 9, 77-127, 1960.
- Koch, G., and A. D. Hershey. Synthesis of phage-precursor protein in bacteria infected with T2. *J. Molecular Biol.*, 1, 260-276, 1959.
- McDonald, M. R. See Kaufmann, B. P.
- Miyake, T. Fertility factor in *Salmonella typhimurium*. *Nature*, 184, 657-658, 1959.
- Miyake, T., and M. Demerec. Proline mutants of *Salmonella typhimurium*. *Genetics*, 45, 755-762, 1960.
- Rudner, Rivka, and Elias Balbinder. Reversions induced by base analogues in *Salmonella typhimurium*. *Nature*, 186, 180, 1960.
- Thomas, R. Effects of chloramphenicol on genetic replication in bacteriophage  $\lambda$ . *Virology*, 9, 275-289, 1959.